



Reproduction  
Deep sea  
Echinoderms  
Molluscs

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Haute mer  
Échinodermes  
Mollusques

# Reproductive variability in deep-sea echinoderms and molluscs from the Rockall Trough

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## ABSTRACT

Recent evidence from long-term monitoring of the deep sea suggest that conditions in this supposedly stable environment may be subject to seasonal forcing. For example, measurements both of flux of particles from the surface and in the velocity of bottom currents suggest seasonal fluctuations occur at the benthic boundary to which the reproductive activity of benthic populations of certain species of echinoderm and bivalve molluscs may be attuned. The small egg size and high fecundity of species showing seasonal periodicities in reproduction suggests planktotrophic development. Larval development occurs in the early part of the year, suggesting that flux of organic particulates from surface production may be an ultimate selective factor for the determination of a reproductive periodicity within the deep-sea environment.

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## RÉSUMÉ

Variabilité reproductive chez les échinodermes et les mollusques de mer profonde dans l'Atlantique nord-occidental (Rockall Trough)

Des résultats récents, obtenus par observation à long terme des eaux profondes, suggèrent que les conditions dans cet environnement prétendu stable, sont en fait soumises à des pressions saisonnières. Par exemple, les mesures de flux particulaire descendant de la surface d'une part, et de flux de particules véhiculées par les courants de fond rapides d'autre part, semblent indiquer que des variations saisonnières interviennent à l'interface benthique, variations avec lesquelles l'activité reproductrice des populations benthiques (c'est-à-dire de certaines espèces d'échinodermes et de mollusques bivalves) semblent en concordance. La petite taille des œufs et la haute fécondité des espèces présentant une périodicité reproductrice saisonnière, suggèrent l'existence d'un développement planctonique. Le développement larvaire se produit au tout début de l'année ; il semble donc que le flux des particules produites en surface soit un facteur fondamental de sélection pour la détermination de la périodicité reproductrice dans l'environnement sous-marin profond.

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## INTRODUCTION

The deep-sea has been considered as one of the most stable, constant and predictable ecosystems at the earth's surface (Bruun, 1957; Menzies, 1965). This constancy in the deep-sea environment is thought to be

reflected in the slow rate of life processes whilst the stability of the deep-sea has been evoked as a factor contributing to the high species diversity (Sanders, 1968). The first unequivocal evidence to challenge the concept of constancy in the deep sea was presented by Schoener (1968) who on the basis of two seasonal samples of adult

ophiuroids suggested a seasonal reproductive periodicity. These initial findings were supplemented by a one-year, five-sample study in the 1 250 m deep San Diego Trough. Rokop (1974) produced evidence of seasonal periodicity in two out of 13 deep sea benthic species. However, these two species had a vertical range that extended into very shallow water. From a more extensive time-series study, Lightfoot *et al.* (1979), Tyler and Gage (1980) and Tyler and Pain (1982 *a*) have shown that there is seasonal reproduction in deep sea brittlestars, seastars and protobranch bivalves.

In addition to these data for reproduction in deep-sea benthic invertebrates, evidence has been produced to show that there is a rapid and seasonal flux of organic matter to the deeper layers from surface primary production (Honjo, 1980; Honjo *et al.*, 1982, Deuser, Ross, 1980, Deuser *et al.*, 1981).

This paper summarises the evidence of seasonal variability, especially reproduction, in the deep-sea and considers some of the factors that have resulted in a rhythmic periodicity in this apparently constant environment.

## MATERIALS AND METHODS

The most detailed examination of reproductive cycles in deep-sea benthic invertebrates has arisen from the deep-sea time-series sampling programme undertaken by the Scottish Marine Biological Association in the Rockall Trough. In 1975 a 2 900 m deep sampling station was established at 54°40'N, 12°16'W and this was supplemented in 1978 by a second station ("M") at 2 200 m depth at 57°18'N, 10°23'W (Gage *et al.*, 1980; Gage, Tyler, 1982). These two stations have been sampled at approximately 4-monthly intervals using either an epibenthic sledge or an Agassiz trawl. Additional benthic samples have been obtained elsewhere in the Rockall Trough, and rectangular mid-water

trawl (RMTI) samples have been obtained over both stations in order to determine the presence of larvae of benthic invertebrates. The reproductive cycles of 17 species of echinoderm have been determined from these samples (Table 1).

## RESULTS

From the available data (Table 1), three distinct reproductive strategies are evident. The more dominant pattern is the production of a few large oocytes c. 900 µm. This is particularly evident in seastars such as *Bathybiaster vexillifer* and *Benthopecten simplex* (Tyler *et al.*, 1982; Pain *et al.*, 1982 *b*). In these species a relatively large number of small oocytes (< 300 µm diameter) are produced. It is possible that some of these oocytes act as nurse cells for those few oocytes that develop to the maximum size of 850 to 1 100 µm depending on species. From this evidence, we may infer that these eggs, once spawned and fertilized, undergo direct development in the benthos, omitting the larval dispersal stage. We have found no evidence of reproductive seasonality in any of the nine seastar species that reproduce by this method. To this group may be added the protandric hermaphrodite brittlestar *Ophiacantha bidentata*.

The second reproductive pattern, and the least common, is that seen in *Ophiomusium lymani* and *Ypsilothuria talismani*. In both these species, the maximum egg-size is c. 400 µm, suggesting a lecithotrophic development with the possibility of a benthic modified larval stage. From the evidence of oocyte size/frequency data, we can see no indication of an annual gametogenic periodicity in either species, although from the evidence of newly recruited juveniles in epibenthic sledge samples, it would appear that there is a seasonal variation in the intensity of recruitment to the adult population of *Ophiomusium lymani* (Gage, Tyler, 1982).

Table 1  
Reproductive biology of deep sea echinoderms from the Northern Rockall Trough.

		Sample depth (M)	Total no examined Female (***)	Male	Max egg size µm	Annual reproductive cycle	Reference
Ophiuroids	<i>Ophiura ljunghmani</i> (*)	2 900	138	132	120	+	Tyler and Gage, 1980
	<i>Ophiomusium lymani</i> (*)	2 200	180	132	420	Only in larval recruitment	Gage and Tyler, 1982
	<i>Ophiacantha bidentata</i> (**) (*)	2 200	211 total		650		Tyler and Gage, 1982 <i>a</i>
	<i>Ophiocten gracilis</i>	1 000	Larvae only		110	+	Tyler and Gage, 1982 <i>b</i>
Asterooids	<i>Bathybiaster vexillifer</i> (*)	2 200	67	51	900		Tyler <i>et al.</i> , 1982
	<i>Psilaster andromeda</i>	2 200	10	12	900		Tyler and Pain, 1982 <i>a</i>
	<i>Plutonaster bifrons</i> (*)	2 200	85	93	110	+	Tyler and Pain, 1982 <i>a</i>
	<i>Dytaster insignis</i>	2 200	6	10	120	? +	Tyler and Pain, 1982 <i>a</i>
	<i>Benthopecten simplex</i> (*)	2 200	90	77	900		Pain <i>et al.</i> , 1982 <i>b</i>
	<i>Pectinaster filholi</i> (*)	2 200	34	31	850		Pain <i>et al.</i> , 1982 <i>b</i>
	<i>Pontaster tenuispinus</i>	590-1 050	17	10	850		Pain <i>et al.</i> , 1982 <i>b</i>
	<i>Pseudarchaster parelii</i>	2 200	7	6	900		Tyler and Pain, 1982 <i>b</i>
	<i>Paragonaster subtilis</i>	2 200	6	15	900		Tyler and Pain, 1982 <i>b</i>
	<i>Zoroaster fulgens</i>	2 200	34	20	900		Pain, personal observation
	<i>Hymenaster membranaceus</i> (*)	2 200	114	104	1 100		Pain <i>et al.</i> , 1982 <i>a</i>
Echinoids	<i>Echinus affinis</i> (*)	2 200	115	121	110	+	Tyler, personal observation
Holothurians	<i>Ypsilothuria talismani</i> (*)	2 200	99	107	400		Tyler and Gage, 1983

(\*) Time series samples. (\*\*) Hermaphrodite species. (\*\*\*) Immature and indeterminate specimens not included.

The remaining five species *Ophiura ljunghmani*, *Ophiocten gracilis*, *Plutonaster bifrons*, *Dytaster insignis* and *Echinus affinis* present the most interesting reproductive cycle. In all species there is a production of a large number of small (c. 110 µm diameter) oocytes. This reproductive pattern in echinoderms is usually indicative of indirect development with a planktotrophic larva as an intermediate stage (Mileikovsky, 1971). However, of considerably more interest is the periodicity of reproduction displayed by these deep-sea species. *Ophiura ljunghmani*, *Plutonaster bifrons* and *Echinus affinis* have been collected regularly enough in the time-series samples to determine their periodicity. In all three species initiation of gonad development occurs in the early months of the year from February to April. Gonad development then proceeds throughout the year until maximum gonad development is found in November-December. Spawning in all three species would appear to occur during January to March, although this period may be extended in the case of *P. bifrons*. Evidence is also available from epibenthic sledge samples as newly recruited juveniles of *O. ljunghmani* and *E. affinis* are taken in epibenthic sledge hauls during the summer months. If we assume that those species undergo planktotrophic development, we may predict a maximum larval period of about four to five months for these species, covering the period of late February to June/July.

Of the two remaining species we have insufficient numbers of adults to determine seasonality. However, in the one large sample of the seastar *Dytaster insignis* all the females are in a similar stage of reproduction. The reproductive seasonality of the brittle star *Ophiocten gracilis* may be determined from the presence in the plankton of its larva *Ophiopluteus ramosus*. This larval form has been retrieved from RMT samples taken in spring during the time-series studies (Tyler, Gage, 1982 b) but also by other workers elsewhere in the North Atlantic Ocean (Mortensen, 1895; Geiger, 1963; Semenova *et al.*, 1964). Benthic postlarvae of this species have been taken in epibenthic sledge samples during the summer months (Gage, Tyler, 1981).

## DISCUSSION

Previous attempts to demonstrate the occurrence of biological variability in the deep-sea have been based on too few samples over too short a time span. Samples must be obtained over at least a one-year period, and if the periodicity is annual, a second and third year's sample is required to validate the data.

As a result of the time-series sampling programme at both the permanent station and station "M" in the Rockall Trough, seasonal samples of echinoderms have become available over a period of 7 and 4 years, respectively. As a result of these collections, and from data presented here and elsewhere (Table 2), we may identify five species that reproduce annually within the deep-sea. Three of these species, *Ophiura ljunghmani*, *Plutonaster bifrons* and *Echinus affinis* show considerable interspecific synchrony of reproduction with spawnout in the early months of the year and recruitment during late spring and summer. *Ophiopluteus ramosus* is found in plankton samples during April and June and post larval ophiuroids of *Ophiocten gracilis* (the adult of *O. ramosus*) and an unidentified echinoid post larva have been found from late May through to August. A fifth species, *Dytaster insignis*, may reproduce seasonally as the only large sample available for this species shows considerable intra-sample synchrony of gametogenesis. One outstanding characteristic of all these species that appear to show this synchrony of reproduction is that all five species form many small (c. 100 µm) diameter eggs, suggestive of a planktotrophic method of larval development for echinoderms.

Other deep-sea species that may show evidence of seasonal reproduction are seen in Table 2. Of particular interest are the time-series samples of the protobranch bivalves *Ledella messanensis* and *Yoldiella jeffreysi*. Both species have very similar reproductive periodicities to that of the echinoderms (Lightfoot *et al.*, 1979). However, these two species probably undergo lecithotrophic development presumably with a non-feeding demersal larva.

Table 2  
Deep sea benthic invertebrates believed to undergo seasonal reproduction.

Species	Area	Depth m	Reference
<i>Storhyngura birsteini</i> (Isopoda)	Drake passage	1 737-3 804	George and Menzies, 1967
<i>Ophiura ljunghmani</i> (Ophiuroid)	Gay Head-Bermuda transect	1 102-3 834	Schoener, 1968
<i>Ophiomusium lymani</i> (Ophiuroid)	—	1 102-2 178	Schoener, 1968
<i>Xylophaga</i> sp. (Bivalve)	180 km S. of Woods Hole	1 830	Turner, 1973
<i>Frieleia halli</i> (Brachiopod)	San Diego Trough	1 250	Rokop, 1977
<i>Cadulus californicus</i> (Scaphopod)	San Diego Trough	1 250	Rokop, 1977
<i>Ledella messanensis</i> (Bivalve)	Rockall Trough	2 900	Lightfoot <i>et al.</i> , 1979
<i>Yoldiella jeffreysi</i> (Bivalve)	Rockall Trough	2 900	Lightfoot <i>et al.</i> , 1979
<i>Ophiocten gracilis</i> (Ophiuroid)	Rockall Trough	1 000	Tyler and Gage, 1982 b
<i>Ophiura ljunghmani</i> (Ophiuroid)	Rockall Trough	2 900	Tyler and Gage, 1980
<i>Plutonaster bifrons</i> (Asteroid)	Rockall Trough	2 200	Tyler and Pain, 1982 a
<i>Dytaster insignis</i> (Asteroid)	Rockall Trough	2 200	Tyler and Pain, 1982 b
<i>Echinus affinis</i> (Echinoid)	Rockall Trough	2 200	Tyler and personal observation

If we assume that there is indeed a synchrony of reproduction with a larval period in the spring, we must consider the selective pressures that have resulted in this reproductive pattern (Table 2). With reference to the San Diego Trough, Rokop (1977) suggested seasonal currents, settling larvae or tidal components as the exogenous factors affecting seasonality. He dismisses food supply from the surface as an unreliable and doubtful cause owing to annual fluctuation in the timing and intensity of surface primary production.

We believe, however, that seasonal input of surface-derived organic matter is the main non-conservative property in an otherwise exceptionally conservative environment. Moseley (1880) proposed that the influx of surface-derived organic matter may influence deep-sea benthic invertebrates, but it has long been considered that the passive sinking of this material was an exceptionally slow continuous process. However, McCave (1975) proposed a mechanism by which organic matter would sink rapidly and field experiments using sediment traps moored at different depths within the deep-sea have shown that the vertical flux of organic matter derived from surface primary production is both very rapid and highly seasonal (Honjo, 1980; Honjo *et al.*, 1982; Deuser, Ross, 1980; Deuser *et al.*, 1981). More recently Billett *et al.* (1983) have shown that there is a seasonal input of surface-derived organic matter to the deep-sea bed in the North-East Atlantic.

If we compare the reproductive life history of these seasonally reproducing echinoderms in the Rockall Trough with surface primary production in the overlying waters, we find that the predicted period of planktonic larval and post larval development coincides with the period of maximum surface primary production (Robinson, 1970). The main flux of organic matter below 2 000 m is < 1.0 mm diameter (Honjo, 1980), and much of the material collected in the sediment traps was < 125  $\mu\text{m}$ . Strathmann (1975) has shown that early developing echinoderm larvae from shallow water populations feed on particles 35-40  $\mu\text{m}$  diameter and that later larval stages feed on particles up to 100  $\mu\text{m}$  diameter. It would appear that these particles selected by echinoderm larvae are qualitatively very similar to those particles found in deep-sea sediment traps, *e.g.*, diatoms, dinoflagellates, coccoliths and small flagellates (Strathmann, 1975; Honjo, 1980; Honjo *et al.*, 1982). We believe, therefore, that the sinking of particulate organic matter, and its associated microflora, acts as a

selective factor for the survival of larvae produced by the deep-sea echinoderms. Larvae produced outside this period are hence unlikely to survive.

Material reaching the sea floor during the summer months is a labile source of organic matter that will provide a suitable energy source for vitellogenesis that occurs during this period. Billett *et al.* (1983) observe that *Echinus affinis* actively forages for this material.

The presence of rapidly sinking organic matter may provide an ultimate selective factor for the periodicity of reproduction in deep-sea echinoderms but it does not explain the factors that stimulate spawning. Recently Dickson *et al.* (1982) showed there is a highly seasonal influx of surface-generated eddy kinetic energy into the deep-sea with maxima in late winter and early spring. Whilst we do not maintain that this directly promotes spawning in deep-sea echinoderms, it is possible that secondary effects such as periodic sediment resuspension at the benthic boundary layer or the rapid transmission of chemical signals may act as the critical factor that stimulates spawning. Although this seasonal variation was observed at all abyssal and bathyal sea floor sites having some degree of bottom slope, it could not be detected on the flat abyssal plains. This may suggest that the populations on a sloping bottom are more likely to be synchronized by this signal than those on the abyssal plains.

Although these hypotheses may explain seasonal reproduction in echinoderms with larval development, more data are required before we can determine the cause of seasonal reproduction in those species that brood as in the isopods (George, Menzies, 1967), or have lecithotrophic development, as in some protobranch bivalves (Lightfoot *et al.*, 1979).

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